THE AFFINITIES OF EARLY ONCOCERID NAUTILOIDS FROM THE LOWER ORDOVICIAN OF SPITSBERGEN AND SWEDEN

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ABSTRACT. *Phthanoncoceras oelandense* gen. et sp. nov. from the Kundan (Llanvirn) of Sweden and *Valhalloceras floweri* gen. et sp. nov. from the Cassinian (Arenig) of Ny Friesland, Spitsbergen are described and a new family, the Phthanoncoceratidae (Oncocerida) is proposed. The relationships of the Phthanoncoceratidae to the Oncocerida and Ellesmerocerida are discussed.

COLLECTIONS of Ordovician cephalopods from the lower Kundan of Öland, Sweden (held in the Swedish Museum of Natural History, Stockholm) and from the Cassinian of Ny Friesland, Spitsbergen (made available by Dr R. A. Fortey) contain two genera showing features intermediate between the Ellesmerocerida and the Oncocerida. These genera, *Phthanoncoceras* gen. nov. and *Valhalloceras* gen. nov., possess thick, layered connecting rings and primary siphonal diaphragms, features considered to be characteristic of the predominantly endogastric Ellesmerocerida. However, both these new genera are exogastric, have relatively narrow, marginal to submarginal siphuncles and conch cross-sections which strongly support an affinity with the Oncocerida. Since it is clear that these genera exhibit mixed characters, the presence of an exogastric curvature is here deemed sufficient to assign *Phthanoncoceras* and *Valhalloceras* to the Oncocerida.

The Graciloceratidae were previously thought to represent the most primitive oncocerids. They have thin connecting rings and lack diaphragms. *Phthanoncoceras* and *Valhalloceras* clearly are not graciloceratids, and the family Phthanoncoceratidae fam. nov. is proposed for these two genera. This new family includes the earliest known oncocerids, and exhibits the retention of primitive features more typical of the Ellesmerocerida.

SYSTEMATIC PALAEONTOLOGY

Order ONCOCERIDA Flower *in* Flower and Kummel, 1950
Family PHTHANONCOCERATIDAE nov.

Diagnosis. Exogastric cyrtocones with depressed to compressed section and a narrow marginal to sub-marginal tubular siphuncle with thickened and layered connecting rings; septal necks orthochoanitic. Siphonal diaphragms present.

Type genus. Phthanoncoceras gen. nov.

Remarks. The Phthanoncoceratidae possess primary siphonal diaphragms and thickened, differentiated connecting rings. They therefore should be assigned to the Ellesmerocerida, themselves diagnosed partly on the possession of such structures (Furnish and Glenister 1964, p. K140). However, in their exogastric curvature, combined with the narrow marginal to sub-marginal siphuncle, the two new genera *Phthanoncoceras* and *Valhalloceras* differ from all other ellesmerocerids. Because of these differences, these two genera are placed in the Oncocerida rather

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than the Ellesmerocerida. The origin of the Oncocerida is unclear and two possibilities require consideration.

Thickened and differentiated connecting rings are a persistent feature throughout most of the Ellesmerocerida. They are also present in the Proterocameroceratidae of the Endocerida and many tarphycerids, including the Basslerocerati dae. Primary siphonal diaphragms are almost entirely associated with late Cambrian cephalopods as well as the Ellesmeroceratidae and Cyclostomiceratidae of the Ellesmerocerida. The possession of thickened connecting rings combined with the presence of primary siphonal diaphragms may indicate that the Phthanoncoceratidae are related to the Ellesmeroceratidae or Cyclostomiceratidae.

Flower (1964, 1968, 1976) and Sweet *et al.* (1964) considered that the Oncocerida originated from the Basslerocerati dae, but the systematic position of the Basslerocerati dae has been disputed. Flower (*in* Flower and Teichert 1957) and Flower (1964) placed the Basslerocerati dae in the Tarphycerida, but Furnish and Glenister (1964) and Balashov (1962) assigned the family to the Ellesmerocerida. Later Flower (1968) argued that placing the Basslerocerati dae in the Ellesmerocerida broadened that order beyond definition. The present authors agree with this latter view, as the Ellesmerocerida already form a large and diverse order.

The Phthanoncoceratidae are similar to the Basslerocerati dae in possessing thick differentiated connecting rings and an exogastrically curved conch. However, to date, it is unknown whether or not the Basslerocerati dae possess primary siphonal diaphragms. The Phthanoncoceratidae differ from the Basslerocerati dae in their narrower siphuncles and more breviconic, rapidly expanding conchs. In the latter feature the Phthanoncoceratidae are thought to have more in common with the Ellesmeroceratidae and Cyclostomiceratidae.

The Phthanoncoceratidae extend the stratigraphical range of the Oncocerida and also modify the way in which the early evolution of the Oncocerida is viewed (see text-fig. 1). Since there is stratigraphical overlap between the Phthanoncoceratidae, Graciloceratidae and Oncoceratidae, it is not clear when the last originated and this family may have a longer history than currently recognized. The existence of thick-ringed oncocerids in strata as young as the early Kundan may also bring into question the relationship of the Graciloceratidae to later oncocerid families. While it is simpler to derive the Oncoceratidae from the Graciloceratidae (e.g. Flower 1976), the same may not be true for the Valcouroceratidae which possess thick, actinosiphonate connecting rings. If the Valcouroceratidae were derived from the Graciloceratidae the connecting rings would have been secondarily thickened, but, if descended from the Phthanoncoceratidae, a thickened connecting ring was already present. Thus it is possible that the Phthanoncoceratidae may, at different times have given rise to more than one oncocerid lineage.

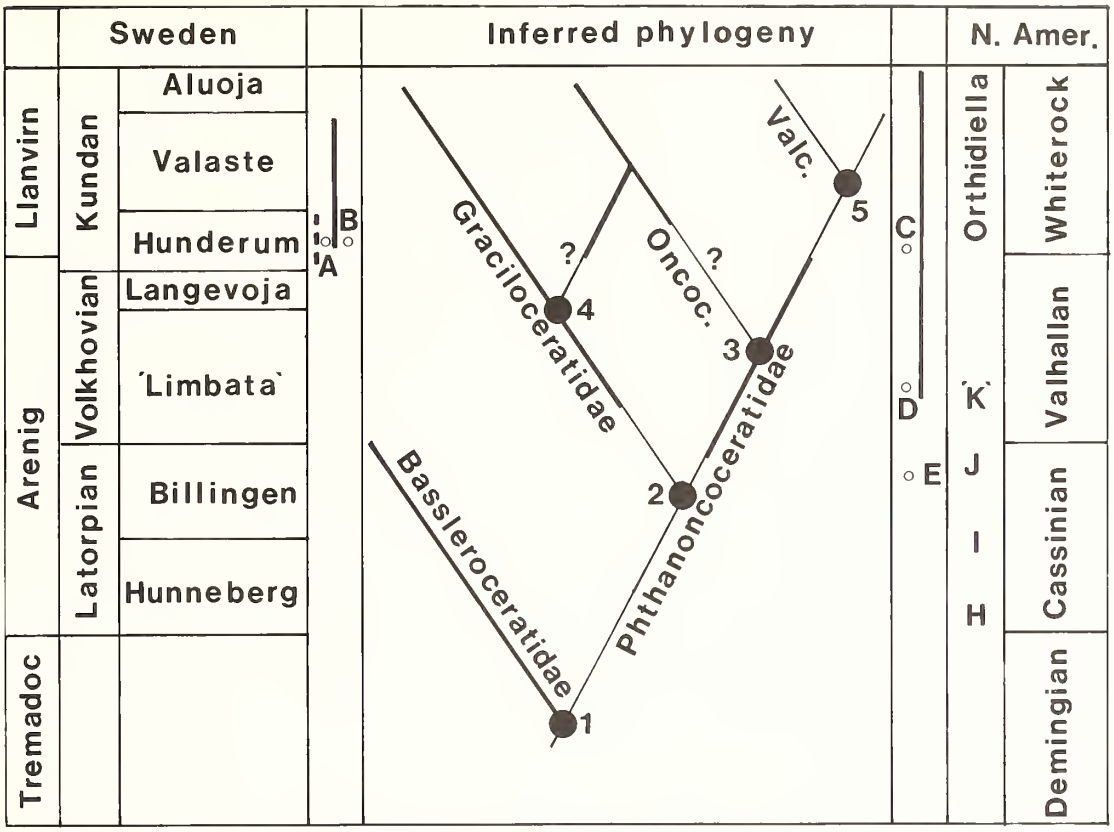
In conclusion, the initial development of the Oncocerida may be the reverse of that which is currently accepted (i.e. derivation from the Basslerocerati dae, e.g. Flower 1976, text-fig. 9) and instead they may have originated from the Ellesmerocerida (quite possibly the Ellesmeroceratidae) through the appearance of exogastric curvature. The Basslerocerati dae and the Tarphycerida formed a lineage derived early in the history of the Phthanoncoceratidae. The Phthanoncoceratidae may themselves have given rise to many of the older oncocerid families through several independent branches (text-fig. 1).

Genus PHTHANONCOCERAS gen. nov.

Type species. Phthanoncoceras oelandense sp. nov.

Diagnosis. Moderately expanding exogastric cyrtocones; body-chamber slightly inflated adapically with shallow constriction near aperture. Conch section laterally compressed with broadly rounded venter and obtusely rounded dorsum. Siphuncle narrow, tubular and sub-ventral. Septal necks orthochoanitic, connecting rings thick and layered; siphonal diaphragms present apically. External shell smooth, growth lines forming a weak ventral sinus.

Derivation of name. From Greek, *phthanein* = to come before.



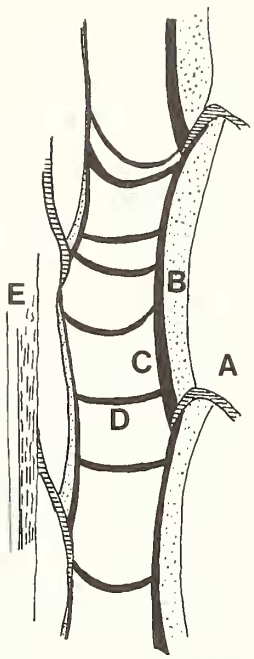
TEXT-FIG. 1. Stratigraphical and phylogenetic relationships of the Phthanoncoceratidae. Chronostratigraphical data based upon Fortey and Bruton (1973), and Jaanusson (1982). Stratigraphical distributions: A, possible range of *Phthanoncoceras oelandense*; B, range of the Graciloceratidae in Öland; C, occurrence of Graciloceratidae (*Leonardoceras* and *Ikesoceras*) in Nevada (Flower 1968); D, occurrence of *Leonardoceras* in Spitsbergen (pers. comm. Dr R. H. Flower to Dr R. A. Fortey 1975); E, occurrence of *Valhalloceras floweri* in Spitsbergen. Synapomorphies: 1, loss of siphonal diaphragms leading to the Basslerocerati dae; 2, loss of siphonal diaphragms and the appearance of thin connecting rings leading to the Graciloceratidae; 3, loss of siphonal diaphragms; appearance of thin connecting rings and development of suborthochoanitic and cyrtochoanitic septal necks (leading to the Oncoceratidae?); 4, appearance of suborthochoanitic and cyrtochoanitic septal necks (leading to the Oncoceratidae?); 5, development of cyrtochoanitic septal necks combined with an actinosiphonate connecting ring leading to the Valcouroceratidae.

Remarks. Phthanoncoceras is a monotypic genus, presently recorded only from Sweden. *Oncoceras*, *Beloitoceras*, *Miamoceras* and *Neumatoceras* (all Oncoceratidae) resemble *Phthanoncoceras* in exhibiting similar conch forms and possessing a constriction on the body-chamber. They differ in having suborthochoanitic to cyrtochoanitic septal necks combined with thin connecting rings. *Valhalloceras* differs from *Phthanoncoceras* only with respect to conch section, which in the former is depressed and subtriangular.

Occurrence. Ordovician, Hunderumian (uppermost Arenig to lowermost Llanvirn) of Öland, Sweden.

Phthanoncoceras oelandense sp. nov.

Plate 1, figs. 1–4.; text-fig. 2



TEXT-FIG. 2. *Phthanoncoceras oelandense* gen. et sp. nov. Camera lucida drawing of adapical portion of preserved phragmocone of Mo158453 showing details of siphuncle and development of diaphragms. A, septal neck; B, spicular layer of connecting ring; C, nacreous layer of connecting ring; D, diaphragm; E, phragmocone wall. × 25.

Diagnosis. As for genus.

Holotype. Swedish Museum of Natural History, Stockholm, Mo158453, collected by G. Holm in 1894 from the 'glaukonit. grå vaginatumkalk' (lower Kundan) at Hälludden. The species is only known from the holotype.

Derivation of name. From Latin, *oelandense* = from Öland.

Description. The type consists of an exogastric, weakly cyrtoconic conch with a moderate expansion rate of 20°. The total length preserved is 53 mm, representing the body-chamber and a portion of phragmocone. Adorally the conch section is compressed with a broadly rounded venter and narrowly rounded dorsum; apically the section is less compressed. External shell ornament consists only of very fine growth lines which form a faint ventral sinus.

The body-chamber has a length of 26 mm with adoral and dorsoventral diameters of 16·9 mm and 14·6 mm respectively. A shallow but broad constriction is present on the internal mould 8 mm from the aperture. The body-chamber is slightly inflated adapically.

EXPLANATION OF PLATE 1

Figs. 1–4, *Phthanoncoceras oelandense* gen. et sp. nov. Hunderumian Substage, lower Kundan at Hälludden, northern Öland, Sweden. 1–3, dorsal, left lateral, and ventral aspects of Mo158453, whitened, × 1·5. 4, sagittal section of Mo158453 showing ventral siphuncle, × 3·75.

Figs. 5–11, *Valhalloceras floweri* gen. et sp. nov. Olenidsletta Member of the Valhallfonna Formation. Adjacent to Hinlopenstreted, North Ny Friesland, Spitsbergen. 5–7, dorsal, right-lateral and ventral aspects of PMO NF2276 and 2285, whitened, × 1·4. 8, 'thick' section of NF2276, right-hand side viewed under reflected light showing submarginal ventral siphuncle, × 3·5. 9, apical surface of NF2285 showing depressed subtriangular section and submarginal septal foramen, venter up, × 4·4. 10, details of siphuncle of NF2276 showing short septal necks and thickened connecting rings represented by dark bands, × 11·7. 11, left-hand side of NF2276, apical camerae with siphonal diaphragms crowded into the siphuncle, × 11·7.

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EVANS and KING, *Phthanoncoceras, Valhalloceras*

The phragmocone consists of fifteen camerae and has an apicad dorsoventral diameter of 6·9 mm. Sutures exhibit weak dorsal and ventral lobes with corresponding lateral saddles. Cameral depth is 20% of the dorsoventral diameter adapically and 12% adorally where septa are approximated. The siphuncle is narrow (about 15% of the phragmocone diameter) and submarginal (0·5 mm to 1·0 mm from the venter). Septal necks are orthochoanitic and 0·3–0·4 mm long. Connecting rings are tubular and layered. Nine closely spaced diaphragms are present in the siphuncle adjacent to the most adapical camerae (see text-fig. 2).

Occurrence. Hunderumian Substage, lower Kundan (uppermost Arenig to lowermost Llanvirn) at Hälludden, northern Öland, Sweden.

Genus VALHALLOCERAS gen. nov.

Type species. Valhalloceras floweri sp. nov.

Diagnosis. Small exogastric conch with subtriangular section, venter obtusely rounded, lateral sides more acutely curved and dorsum broadly rounded. Siphuncle narrow, subventral, orthochoanitic; connecting rings thickened and differentiated; siphonal diaphragms present. Sutures consist of weak dorsal and ventral lobes with lateral saddles. Shell smooth, weak sinus over venter.

Derivation of name. After the Valhallfonna Formation, from which the type species was collected.

Remarks and occurrence. Valhalloceras is at present known only from Spitsbergen in facies belonging to the Nileid Association of Fortey (1975). *Valhalloceras* shows many similarities to *Ikesoceras* Flower in terms of gross conch morphology; however, it is unknown whether the latter possesses siphonal diaphragms. The holotype of *Ikesoceras* (Flower 1968, p. 25, pl. 25, figs. 1–5) consists of a body-chamber and the four most adoral camerae, too far adoral to exhibit siphonal diaphragms. The paratype (Flower 1968, pl. 26, figs. 6 and 7) is partly crushed and silicified and represents an adapical portion of phragmocone which, on the basis of *Valhalloceras floweri*, might contain siphonal diaphragms. None have so far been demonstrated. *Valhalloceras* came from a horizon near the top of the Olenidsletta Member of the Valhallfonna Formation, dated as Cassinian J Zone (Cooper and Fortey 1982, fig. 2) and is older than *Ikesoceras* (early Whiterockian zone L *sensu* Cooper and Fortey 1982; Fortey and Owens 1987). *Ikesoceras* appears to occur in a similar facies to *Valhalloceras*, considered to represent the outer lip of the shelf of Ross (1975) and equivalent to the upper slope of Shaw and Fortey (1977), or the Nileid Association of Fortey (1975). Until *Ikesoceras* is better known its systematic position will remain uncertain. However, should *Ikesoceras* prove to possess siphonal diaphragms good reason will exist for regarding it as a senior synonym of *Valhalloceras*.

Valhalloceras floweri sp. nov.

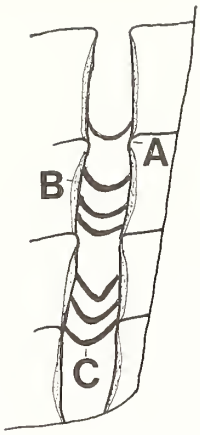
Plate 1, figs. 5–11; text-fig. 3.

Diagnosis. As for genus.

Holotype. Palaeontological Museum, Oslo NF2276, 2285. These represent complementary fragments of the same specimen. NF2276 was prepared as a thin section, but has been left thick as the siphuncle was displaced in the most apical portion. It was this portion which contained siphonal diaphragms, further preparation of the section would have destroyed these structures. The species is only known from the holotype.

Derivation of name. In honour of the late Dr R. H. Flower.

Description. PMO NF2276 and 2285 represent a portion of phragmocone 44 mm long, slightly crushed adorally. Adapically the cross-section of the conch is almost elliptical with lateral and dorsoventral diameters of 6·4 mm and 5·0 mm respectively. At a position 17·5 mm adorally the cross-section is subtriangular, with the maximum lateral diameter (11·0 mm) 40% of the distance from venter to dorsum (dorso-ventral diameter



TEXT-FIG. 3. *Vallhalloceras floweri* gen. et sp. nov. Camera lucida drawing of adapical portion of phragmocone of NF2276 showing details of siphuncle and development of diaphragms. A, septal neck; B, connecting ring; C, diaphragm. ×9.

9·1 mm). A further 15 mm adorally the lateral diameter is estimated to be 16·0 mm. Cameral depth is 17% of the dorsoventral diameter adapically and 13% adorally. The suture comprises weak dorsal and ventral lobes and lateral saddles. Where the conch wall is preserved, it is smooth, consisting of very fine growth lines which trace out a shallow ventral sinus.

The siphuncle is submarginal, its centre being positioned 15% of the distance from the venter to the dorsum; it is 9% of the dorso-ventral diameter. Septal necks are orthochoanitic and about 0·3 mm long. Connecting rings are tubular and consist of two layers; a very thin light coloured dense layer lining the siphonal cavity and a thicker, darker, more diffuse layer forming the cameral side of the connecting ring. In the four most adapical camerae eleven closely spaced diaphragms are present in the siphuncle.

Occurrence. From the outcrop of the Olenidsletta Member between Lundehuken and Papegoyneset, adjacent to Hinlopenstreted, North Ny Friesland, Spitsbergen. The stratigraphical horizon is *c.* 100 m above the base of the Olenidsletta Member of the Vallhalfonna Formation at the top of V_2 in the terminology of Fortey (1980) and Arenig Series Ca 1 in terms of graptolites (= North American *D. bifidus* Zone, see Cooper and Fortey 1982, fig. 2).

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